GROWTH ANALYSIS OF HYBRID DIGITGRASS 'X46-2' SWARD

By

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Abstract of Dissertation Presented to the Graduate Council of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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Frequent defoliations of swards may affect forage yield or its quality. In order to determine growth responses of an established digitgrass sward to different harvest intervals, digestibility of the forage produced, and to relate regrowth following defoliation to carbohydrate reserves, a growth analysis of hybrid digitgrass 'X46-2' Digitaria sp. (PI # 299892) ♀ and Digitaria valida Stent. (PI # 299850 ♂) sward established in a loamy fine sand soil near Gainesville, Florida, was studied from July to November 1977. Initially, the sward was mowed to a 10-cm stubble height; it was then fertilized with 60 kg of N/ha at 4-week intervals. Three frequencies of defoliation were imposed in four replications, resulting in four (A1, A2, A3 and A4), three (B1, B2 and B3), and two (C1 and C2) regrowth cycles under 4-, 6- and 8-week harvest frequencies, respectively. Four samples of 0.25 m^2 were clipped weekly at ground level for dry matter yield determinations. Two of these were cut in 10-cm layers, except during cycles A1, B1 and C1. From one sample, subsamples were taken for leaf area measurements. Samplings to quantify

total nonstructural carbohydrates (TNC) of stem bases were taken at frequencies of zero, 2, 5 and 7 days, and then at each subsequent week until the end of each regrowth cycle. IVOMD was determined in all standing biomass at the end of each cycle, and weekly in the herbage from each layer in all cycles. Crop growth rate (CGR) decreased as the season progressed as a consequence of decreased effective growing degrees, and decreased rainfall during the experimental period. The efficiency of regrowth (RGR) decreased drastically from 0.56 to 0.13 g/g/week during the growing period. Leaf area index (LAI) increased linearly until the fourth week in all cycles, after which it declined. Net assimilation rates (NAR) varied from 0.54 to 0.31 g/dm^2/week. Highest values always occurred during the first week of regrowth, whereas the lowest were observed at the end of most regrowth cycles. Nitrogen fertilization and defoliations induced depletion of TNC concentrations of stem bases. TNC concentrations declined from 17.0 $\pm$ 4.9 to 9.2 $\pm$ 3.1% during the first 5 days of regrowth. Herbage IVOMD varied from 61 to 48% in total standing biomass at the end of regrowth cycles. Highest values occurred at the end of cycles under 4-week harvest intervals. Lowest values occurred at 0 to 10 cm layers (43%), whereas digestibilities greater than 70% were observed in the upper layers. Total yields of dry matter were 7,650, 8,870 and 8,460 kg of DM/ha at 4-, 6- and 8-week defoliation frequencies, although only 4,110, 4,480 and 3,870 kg of organic

matter per hectare, respectively, were digestible. Correlation coefficient (r) between dry matter produced and effective growing degrees was 0.91 ($P<0.01$), and between dry matter produced and rainfall was 0.83 ($P<0.01$).

CHAPTER I

INTRODUCTION

While it is generally recognized that tropical pastures have a high potential for production, the physiological and ecological bases of this potential have not been sufficiently studied.

Among others, the digitgrasses (Digitaria sp. Haller.) play an important role in the livestock industry of tropical and subtropical regions of the world. Yet, limited information is available regarding their management under grazing conditions or hay production.

Several management factors and responses under field conditions should be studied, such as the length of rest period, carbohydrate reserves in stem bases, leaf and stem production and their distribution in the canopy, and the association of these factors with environmental conditions surrounding the plant community. The quality of the forage produced must also be known to develop a rational pasture management scheme in order to achieve high productivity.

As quite properly stated, one should not lose sight of the importance of a knowledge of the physiological functions

of grass plants, particularly assimilation, translocation and accumulation of CH_2O and their remobilization and utilization. Research work on the morphological and physiological aspects of grass growth should go hand in hand if the interpretation of treatment effects is to have a firm scientific basis (Booysen et al., 1963).

A growth analysis was made in an established sward of hybrid Digitgrass 'X46-2' subjected to three defoliation frequencies. The forage produced during the season, its distribution in different layers of the canopy; the carbohydrate reserves at stem bases and their influence on sward regrowth; and the relationships of these parameters with effective growing degrees and rainfall were studied in an effort to generate information for rational pasture management systems.

CHAPTER II

LITERATURE REVIEW

Effects of Environmental Factors Upon Forage Species

Response to Light Energy

The dry matter production of actively growing plants is limited by the interception and utilization of light. Moreover, success and survival of individuals in these communities depend upon how they intercept, compete for and respond to light. Light regimes and pasture canopies are influenced by atmospheric conditions, and the nature, size, and structure of the canopy. As light passes through a canopy of chlorophyll-bearing tissue, it gets progressively altered in quality and reduced in quantity. The increase in infra-red with depth in canopies, potentially, can have profound effects on growth and development. Shading reduces photosynthesis and growth; it alters plant development and dry matter production (Ludlow, 1978).

The photosynthetic efficiency of temperate plant communities has been shown to be inversely proportional to incident solar radiation. However, in tropical grass communities, photosynthetic efficiency is maintained at higher solar

irradiations, indicating a continuing photosynthetic response at these high levels of solar irradiation (Cartledge and Connor, 1973). Besides light intensity, duration of light incident alters tropical plant performances. Mannetje and Pritchard (1974) reported decreased yields of 8 tropical grasses and 11 tropical legumes when the day length was decreased from 14 to 11 hours of light energy.

Light response curves of C_3 species (those containing only the Calvin photosynthetic pathway) have a lower initial slope (Cooper and Tainton, 1968), or lower photosynthetic efficiency, than those of C_4 plants, which contain both C_3 and C_4 photosynthetic pathways (Hatch and Slack, 1967). These curves for C_3 species show light saturation at 30 to 50% of full sunlight illuminations, while, in the absence of environmental or physiological limitations, light response curves for C_4 plants do not saturate at full sunlight illuminations (Cooper and Taiton, 1968; Ludlow and Wilson, 1971). This occurs because C_4 plants have lower intracellular and stomatal resistances, which decline progressively with increasing illumination, and not because of particular photochemical and biochemical characteristics of C_4 syndrome, as is so often stated (Ludlow, 1978).

Light becomes attenuated as it penetrates a foliage canopy and, if sufficiently reduced, may impair the function and development of lower story shoots that become excessively

shaded in comparison with their performance in unshaded conditions. The extent of these effects will depend on the stage of development of the plant and degree of shading, bearing in mind that reduced light level in the canopy is not uniform over the whole plant (Rhodes, 1978). The proportion of leaves in Panicum maximum Jacq., Brachiaria ruziziensis Germain & Evrard, Calopogonium mucunoides Desv., and Macroptilium atropurpureum (DC.) Urb. increased when grown at higher relative illuminations (Ludlow et al., 1974). However, the dry weight of all species was depressed by shading. This effect was specially marked in the grass species. Similar decrease in dry weight of three tropical grasses and three tropical legumes due to shading was also reported by Heslehurst and Wilson (1974).

Response to Temperature

Temperature is a major factor controlling the distribution and diversity of pasture plant species. One important feature of tropical pastures, that distinguishes them from temperate ones, is their higher temperature range for growth and development (McWilliam, 1978). For most temperate Festucoid grasses, including Lolium perenne L., Dactylis glomerata L., and Phleum pratense L., the optimum temperature for growth lies between 20 to 30°C. The growth rate drops rapidly below 10°C, but there is still some growth at 5°C,

and the plant remains healthy. Even with ample water supply, growth is reduced at temperatures above 25°C, and may cease above 30 to 35°C (Cooper and Tainton, 1968). Subtropical and tropical Panicoid grasses have much higher optimum temperature for growth. Such species as Panicum maximum (McKosker and Tietzel, 1973), Melinis minutiflora Beauv., Hyparrhenia rufa (Nees) Stapf. (Pedreira, 1973), and Digitaria decumbens Stent. (Karbassi et al., 1972; Chatterton et al., 1972; Garrard and Carter, 1976; Carter and Garrard, 1976), will present optimum growth in the vicinities of 35°C, if other factors—light, soil moisture, nutrients, etc.—are not limiting. The upper limit for growth and development is approximately 40 to 40°C, and little or not growth occurs below 15°C. Tropical legumes appear to have slightly lower optimum temperatures (25 to 30°C), although the minimum temperature for growth (15°C) is similar for both groups (Ludlow and Wilson, 1970a; Whiteman, 1968; Whiteman and Lulham, 1970).

The plant growth in response to temperature depends to some extent on the stage of ontogeny. Young plants tend to have a higher optimum temperature, which declines with age because of the increasing importance of dark respiration (Friend et al., 1962). During the early stage of growth of swards, the rate of canopy development is favored by high temperatures. However, with time and increasing plant maturity these conditions cause accelerated leaf senescence

(McWilliam, 1978), while total leaf area development is favored by lower temperatures. Lower temperature under these conditions delays leaf senescence and reduces respiration, which increases the availability of carbohydrates for both root and shoot development (Alberda, 1957, 1965; Ryle, 1964).

The optimum temperature for photosynthesis increases with an increase in either CO_2 concentration or irradiation, which suggests that temperature operates primarily through its effect on the biochemical reactions involved in carbon fixation, and that these are important rate-limiting steps under those conditions (Ludlow and Wilson, 1971). This view is supported by the evidence that the maximum specific activity of the primary carboxilating enzyme in C_3 and C_4 plants is found at temperatures close to those giving maximum rates of photosynthesis (Treharne and Eagles, 1970).

One of the important consequences of increased temperature is the exponential increase in the rate of dark respiration. This causes a reduction in growth through the accelerated aging of leaves, and the exhaustion of carbohydrate reserves (Smith and Jewiss, 1966; Baker and Jung, 1968a, 1968b).

Response to Water

While temperature is the major factor controlling the distribution and diversity of pasture plant species

(McWilliam, 1978), soil moisture is the major factor limiting pasture growth in tropical and subtropical regions throughout the year (Fitzpatrick and Nix, 1970; Smith and Stephens, 1976). Pastures of tropical regions depend largely on rainfall for their source of water and, where rainfall is irregular, water deficits develop, which can severely limit productivity and persistence (Turner and Begg, 1978).

Fitzpatrick and Nix (1970), using a model which included the three major climatic factors—light, temperature and water—showed the cyclic variability of available soil water could be the most important factor controlling growth of pasture in the semi-arid tropics of Australia. A single model for predicting pasture growth from climatic data was, also, developed and tested against experimental data in New South Wales (Smith and Stephens, 1976). Soil moisture, again, was the major factor limiting pasture growth from early October until late May, and temperature was the major factor from the end of May to early October. The period May through October was a time when both factors had similar probabilities of being the most limiting factor.

Evaporative demand in the tropics tends to exceed rainfall during the summer, therefore, soil moisture becomes the limiting factor. The reverse situation may occur during the winter, when temperature often limits pasture growth (Begg, 1959; Smith and Johns, 1975). Evaporation is an energy-dependent process involving a change in state from

liquid to vapor phase. The actual rate of evapotranspiration from the plant community is a function not only of the available energy, but also the vapor pressure gradient, and the ability of the soil and plant to transport water to the sites of evaporation. In unstressed plants, evaporation is largely governed by meteorological conditions in the atmosphere external to the soil-plant system, but the plant does exercise some control over water loss through its stomatal and cuticular resistances in the water pathway (Turner and Begg, 1978).

The growth and development of a plant depends on continuing cell division, on the progressive initiation of primordia, and on the differentiation and enlargement of cells (Slatyer, 1967). One of the most important consequences of the sensitivity of cell enlargement to small water deficits is the marked reduction in leaf area, and the resulting reduction in growth rate, particularly where there is an incomplete light interception. Water stress can also affect leaf area by reducing tillering, and by hastening the death of leaves and tillers (Turner and Begg, 1978).

The water use efficiency of C_4 species is generally twice that of C_3 plants (Ludlow and Wilson, 1972; Slatyer, 1970; Teare et al., 1973). This arises from the generally higher photosynthetic capacity of C_4 species, particularly under high light and temperature conditions, and due to the

higher stomatal resistance resulting in relatively less transpiration (Turner and Begg, 1978).

Growth Analysis of Forage Species

The quantitative analysis of plant growth has been widely studied by plant physiologists throughout the world, in an attempt to explain biological features of plant growth and development, or to determine managerial practices to profitable crop production. The basic concepts of growth analysis and its physiological or ecological implications are quite simple, and well explained in the literature (Blackman, 1919; Briggs et al., 1920a, 1920b; Evans, 1972; Fisher, 1920; Heath and Gregory, 1938; Ludlow and Wilson, 1968; Watson, 1952; Whitehead and Meyerscough, 1962; Wilson, 1966). These authors discussed several parameters such as crop growth rate (CGR), relative growth rate (RGR), net assimilation rate (NAR), and leaf area index (LAI), as useful indexes in comparing individual plant or community performances.

Two assessments are required to carry out a simple growth analysis (Radford, 1967). If the plants being studied form a continuous canopy cover, such as a sward, the relevant measurements are (1) the total dry weight of plant biomass per unit area of ground and (2) the total leaf area of plant material per unit of soil surface.

Crop growth rate (CGR) has been defined as the increase in dry weight (W) over a time interval (t), thus CGR = dW/dt. The mean CGR over a time period from t_1 to t_2 is given by

$$\overline{CGR} = \frac{1}{t_2-t_1} \int_{t_1}^{t_2} \frac{dW}{dt}\, dt \qquad \overline{CGR} = \frac{W_2-W_1}{t_2-t_1}$$

where W_1 and W_2 are the values of W at times t_1 and t_2, respectively. The only assumption necessary to carry out this integration is that W varies without discontinuity throughout the period t_1 to t_2. CGR may be expressed as g/m^2/week, or kg/ha/week, depending upon the purpose of the investigation.

Relative growth rate (RGR) has been defined as the increase in dry weight (W) per unit of original weight, over a time interval (t), thus, RGR = 1/W x dW/dt. The mean RGR over a time period from t_1 to t_2 is given by

$$\overline{RGR} = \frac{1}{t_2-t_1} \int_{t_1}^{t_2} \frac{1}{W} \times \frac{dW}{dt} \qquad \overline{RGR} = \frac{\log_e W_2-\log_e W_1}{t_2-t_1}$$

Again, the only assumption necessary to carry out this integration is that W varies without discontinuity throughout the period t_1 to t_2, no matter how W or RGR change linearly or exponentially with time. RER is considered as an index of

efficiency of plant growth, and usually declines later in the plant's life cycle. It is usually expressed as g/g/day, or g/g/week.

Net assimilation rate (NAR), or unit leaf rate, has been defined as the rate of increase in dry weight (W) per unit of leaf area (L) per unit of time (t). Thus, NAR = 1/L x dW/dt. The mean NAR over a period from t_1 to t_2 is given by

$$\overline{NAR} = \frac{1}{t_2-t_1} \int_{t_1}^{t_2} \frac{1}{L} \times \frac{dW}{dt} \, dt.$$

However, this integration only can be carried out if W and L are continuous functions of time, and the relationship between L and W are known. If W is linearly related to L, the mean NAR is given by

$$\overline{NAR} = \frac{W_2-W_1}{L_2-L_1} \times \frac{\log_e L_2-\log_e L_1}{t_2-t_1}$$

where W_1 and W_2 are the values of W, and L_1 and L_2 are the values of L at times t_1 and t_2, respectively. On the other hand, if W varies with the square of L, then

$$\overline{NAR} = \frac{2(W_2-W_1)}{(L_2-L_1)(t_2-t_1)} .$$

Nevertheless, if W is curvilinearly related to L as in the function $W = a + bL + cL^2$, then

$$NAR = \frac{b(\log_e L_2 - \log_e L_1)}{t_2 - t_1} + \frac{2c(L_2 - L_1)}{t_2 - t_1}$$

where b and c are the regression coefficients of the quadratic function. NAR is often expressed as $mg/cm^2/day$, or as $g/m^2/week$ which is perhaps the most convenient for ecologists and agriculturalists (Coombe, 1960).

Leaf area index (LAI) has been defined as the ratio of leaf area to the soil area it occupies. It is unitless since one may express LAI as cm^2 of leaves over cm^2 of ground surface; or m^2 of photosynthetizing tissues over m^2 of supporting land. The LAI concept in pasture growth was reviewed by Brown and Blaser (1968), where the complexities of light interception by the canopy, the assimilation and consequent growth responses to LAI, and the regrowth following defoliations are extensively discussed.

Brougham (1956), in his classical work with a pasture association comprising short-rotation ryegrass, red clover and white clover subjected to 3 intensities of defoliation, observed that when the pasture was defoliated to 2.5 cm height, light interception was almost complete (95% or over) approximately 24 days after cutting; whereas pasture defoliated to 7.5 and 12.5 cm height intercepted almost all

the incident light 16 and 4 days after cutting, respectively. At this stage (95% of light interception), the LAI was approximately 5 and the herbage yield around 1600 kg DM/ha regardless of treatment. Dry matter yield increased linearly with an increase in LAI. The regression coefficient was 468 $\pm$ 28. The interpretation being that an increase of 1 m^2 of leaf area was accompanied by an increase in herbage yield of 468 kg of DM/ha over the range of these data. Brougham (1968) extended his work questioning the relationships between light interception and LAI in the regrowth of pure stands of short-rotation ryegrass, perennial ryegrass, timothy, white clover, and a mixed stand of short-rotation ryegrass and white-clover. The critical LAI (LAI at which 95% of the incident light is intercepted) about midday in mid-summer were as follows: short-rotation ryegrass 7.1, perennial ryegrass 7.1, timothy 6.5, white clover 3.5, and for the mixed stand 4.5. The author also observed that the percentage of light penetrating through the foliage on cloudless days in summer changed considerably with the time of day. The highest values were recorded at noon, and the lowest 2-3 hours after sunrise and before sunset. These results were attributed to the angle of incident of light, and suggested marked seasonal differences in the leaf area required to intercept 95% of the light. It was also suggested that mid-winter values are approximately one-half of mid-summer values.

The growth of Trifolium subterraneum L. sown at different densities and subjected to defoliations at various dates was studied by Davidson and Donald (1958). The rate of dry matter production of this legume increased to a maximum when LAI was about 5, falling by about 30% as the LAI increased to 8.7. Therefore, there is evidence that the rate of dry matter production by crops or pastures will increase as the LAI increases, until a maximum value is attained; thereafter, as the index increases further, the rate of dry matter production will decline. This is presumed to occur because the lowermost leaves become so heavily shaded at high LAI that their photosynthetic contribution is less than their respiration (Stern and Donald, 1961).

Some experiments have shown an optimum LAI, while others have not. There are two reasons for this (McCree and Troughton, 1966). First, the models predict the net rate of synthesis of material, i.e., the production rate. In order to obtain this by harvesting, it is necessary not only to harvest the whole plant, but also to include all material which dies between harvests. The models do not predict the rate of synthesis minus the rate of death. Second, since the models deal only with the light factor, all other factors which might affect net photosynthesis must be kept constant.

It should always be remembered, when determining leaf area, that the leaves are losing water and that they may be

shrinking during the period between cutting and the completion of area determining process. The process should be as quick as possible and the leaves should be kept in a polythene bag to minimize water losses. The extent of shrinkage varies among species, being a function both of the extensibility of the leaf cell walls, and the leaf architecture (Evans, 1972).

The usefulness of comparisons of growth analysis components between species, whether within or between family groups, is limited by some considerations (Ludlow and Wilson, 1970a). Firstly, in any species, RGR, NAR and LAR (leaf area ratio) are known to bear a relationship which is characteristic for a given radiation environment, but comparisons in one environment may be very different from that in another. Secondly, there are usually important drifts in NAR and LAR which in turn affect RGR; and these vary with species. The relative values for species will then depend on the particular age at which comparisons are made. NAR is known to change with age (Thorne, 1960); here two factors may be of importance: 1) mutual shading may reduce the average photosynthetic activity, and 2) leaves reach their maximum in photosynthetic capacity fairly early and, subsequently, decline which causes decreased mean photosynthetic rates.

NAR is the growth component which can be compared with the greatest reliability. As a general rule, NAR values depend almost entirely on leaf activity (Ludlow and Wilson,

1970a). It is clear that NAR has a great advantage over other measures of growth in that, for much of time and for many species, it is highly dependent on environmental factors and less dependent on internal factors. If two species show different values of NAR in one environment at the same time, they will probably also differ to the same extent and direction at another time. The same cannot be said of comparisons of their RGRs (Coombe, 1960). Therefore, RGR reflects the inherent efficiency of the growth process irrespective of plant size and provides a good basis for comparing treatment effects (Booysen and Nelson, 1975).

Comparisons of the productivity of Panicum maximum cv. 'Hamil' and Macroptilium atropurpureum cv. 'Siratro' were made in Australia by Ludlow and Wilson (1968) using the RGR, NAR and LAR concepts. Later, the same authors (Ludlow and Wilson, 1970a) discuss the behavior of 20 tropical grass and legume species using the same growth parameters. Booysen and Nelson (1975) discuss the RGR and LAI in an experiment with Festuca arundinacea Schreb. as affected by carbohydrate reserves. Net assimilation rates and other growth attributes were examined by Wilson (1966) for rape (Brassica napus L. cv. 'Giant'), sunflower (Helianthus annus L. cv. 'Jupiter') and maize (Zea mays L. cv. 'Standfast') plants growing widely spaced at temperatures of 10, 16, 22, 28 and 34°C.

Response of Forage Plants to Defoliation

In most exploratory agronomic pasture studies, it is usually convenient to use small experimental plots under clipping regimes. Such trials are precise and give useful indications of the differences among pasture treatments.

There are three main points requiring detailed investigations for each species making up the sward: 1) the time of elevation of the shoot-apex and the duration of its accessibility to the grazing animals; 2) the capacity of these species for producing reproductive tillers as measured by the ratio of reproductive to vegetative tillers; and 3) the capacity of the plant to produce lateral tillers from axillary meristems. Once these factors have been established, it becomes necessary to investigate the influence of various defoliation treatments on these properties of the plant. However, even at this stage it will be difficult to make accurate predictions of the influence of management on the developmental processes of plants without a careful study of the environment (Booysen et al., 1963).

Branson (1953) concluded that a measure of the resistance of grasses to defoliation can be gained by determining the length of time that shoot-apex is elevated and accessible to the animal, and the fertile to sterile stem ratio characteristic of the species. Susceptibility to grazing is correlated to duration of accessibility of apical buds, and to fertile/sterile stem ratio. He found that in

Panicum virgatum L. plants the vegetative growing points are elevated well above the soil level early in the season and that this grass is characterized by the fertile/sterile stem ratio of about 2:1. The percentage of this grass making up any particular sward was found to decrease rapidly under grazing and it was found to be absent in ranges in poor conditions. As opposed to this grass, the growing points of Andropogon gerardi L. remained below ground level until late in the season, but it also had a higher fertile/sterile stem ratio of 3:1. On the other hand Poa pratense L. plants proved to be extremely resistent to grazing as not only did the buds remain just below the soil surface throughout the season, but, in addition, the fertile to sterile stem ratio was extremely low (1:10).

If maximum dry matter production was the sole objective determining management decisions involving defoliation, then two criteria would apply (Harris, 1978). Firstly, defoliation frequency should be such that regrowth interval is extended until pasture growth rate begins to decline from its maximum. Secondly, the intensity of defoliation should be to the level that leaves the amount of biomass at which maximum growth rate is first attained.

Complete defoliation seldom occurs under grazing pressures which favors both yield and animal product per area and longevity of grass sward. Generally, some tillers are only partially grazed or escape defoliation entirely. As

they age, these tillers become less palatable to livestock; consequently, cattle may selectively graze the more palatable regrowth made by the closely defoliated ones. These tillers which were not defoliated may influence the regrowth of others closely defoliated. Matches (1966) simulated this situation in a stand of Festuca arundinacea leaving 0, 10, 20 or 30% of uncut tillers after defoliations at 2.5, 6.25 and 10 cm height. Increased tillering, and greater daily and total dry matter yield resulted from increasing the height of stubble or from leaving intact tillers. Apparently, 10% or more intact tillers, or 10-cm stubble provided adequate photosynthate production and food reserve storage for plant survival and growth under conditions of defoliation stress. However, in a greenhouse experiment with Paspalum dilatatum Poir. cut at stubble height of 2.5 and 7.5 cm in a factorial combination of 0, 10, 20 and 30% of intact tillers, Watson and Ward (1970) had a contrasting conclusion with respect to stubble height. The dry matter yield of dallisgrass decreased with an increase in stubble height; however, it increased with an increase of intact tillers left after the previous harvesting. The response of four tropical grasses at two cutting heights (5 and 15 cm) and at three harvesting intervals (30, 45 and 60 days) were investigated by Sotomayor-Rios et al. (1974) in Puerto Rico. At all harvest intervals, the grasses produced more total yield when cut to a height of 5 cm than when cut at 15 cm above

ground. The overall means for all grasses and cutting heights were, approximately, 26,400, 22,300 and 17,300 kg of DM/ha when cut at 60, 45 or 30 day intervals, respectively. Similarly, the yields of a Pensacola bahiagrass sward clipped monthly from June to October, in Georgia, were 7,680 and 2,680 kg DM/ha when cut at 2.5 and 7.5 cm respectively (Beaty et al., 1977).

Carbohydrate Reserves in the Regrowth of Forage Species

Defoliation of grasses restricts tillering, root growth and accumulation of total nonstructural carbohydrates (Youngner, 1972). As a rule, the more intense the defoliation, the more severe these effects.

Numerous investigations have shown that cutting of herbage plants invariably causes a decrease in the amount of total nonstructural carbohydrates (TNC) in the remaining plant parts (Alberda, 1966; Bender and Smith, 1973; Blaser et al., 1966; Bommer, 1966; Ojima and Isawa, 1968; Ward and Blaser, 1961; Wilson and Ford, 1973). This decrease reaches a minimum about 1 week after cutting, and it is followed by an increase associated with increasing photosynthetic activity (Alberda, 1966). If cutting is repeated before the original TNC level is restored, the successive herbage yields will become smaller and, eventually, such treatment will lead

to the death of the plant. It seems logical that the initial regrowth of defoliated forages must depend on carbohydrate (CH_2O), but subsequent growth is associated with photosynthesis by new leaves. Blaser et al. (1966) clearly asserted that the separation of effects of leaf area and CH_2O in regrowth is not likely to be fully accomplished, since the leafage remaining after defoliation absorbs light energy, but also contains CH_2O which may supply energy and materials for regrowth; conversely, when rapid initial regrowth is attributed to high levels of CH_2O, early leaf formation immediately becomes a confounding factor.

The major storage areas of CH_2O reserves in perennial grasses are usually the lower regions of stems, which includes stolons, corms or rhizomes, and not in the roots per se. The decrease of CH_2O reserves in the roots of Dactylis glomerata, after severe defoliation, accounted for less than one-tenth of root respiration (Davidson and Milthorpe, 1966).

Effect of temperature

The effect of temperature on the percentage of CH_2O reserves in the stem bases varies according to the origin of grass species. This difference in optimum temperature is directly related to the characteristic enzymatic system in each type of grasses, to the stomatal behavior, and to several physiological features.

Thirteen tropical and subtropical grasses and 11 temperate grasses were grown in controlled environment under day/night temperatures of 21/13, 27/19 and 32/24°C (Wilson and Ford, 1973). Each plant was harvested 2 days after the fifth leaf on the main stem reached maximum length. The content of CH_2O was much higher for the temperate than the tropical group, and it decreased with increasing temperature, this effect being more accentuated in the temperate species. The TNC of three cultivars of bermudagrass (Cynodon sp.) increased slightly in the sprigs of all bermudagrass cultivars from early to late fall, but decreased during the winter (Dunn and Nelson, 1974). This trend appears to coincide with the pattern of cold hardening of bermudagrasses. The decrease in TNC levels was probably caused by slow respiration during the winter, while no additional CH_2O was being manufactured by frost-killed leaves. Starch and TNC increased in Zoysia japonica L. (Rogers et al., 1975), a warm-season turfgrass species, during September and remained at relatively high levels until December. Later, starch and TNC decreased about 80% from December to March.

Noble and Lowe (1974) determined the CH_2O content of Lolium perenne and Bromus unioloides Kunth (temperate species), Setaria anceps Stapf ex Massey. and Panicum maximum (tropical species), during 2 years with monthly samplings. The total alcohol-soluble CH_2O levels of temperate species varied from 3 to 9%, while the variation in the tropical species

was from 2.5 to 4.0%. There were few significant differences between levels in Setaria anceps and Panicum maximum in summer, but larger differences were recorded in autumn and winter. In the temperate grasses, the levels were higher in late spring and midwinter, but lower in summer and early fall.

Effect of Nitrogen on CH_2O Reserves

Nitrogen applied at low levels often increases CH_2O reserves, but at high rates it will deplete it. Increased plant growth by N applications is associated with increased leaf area, chloroplast protein and chlorophyll pigments. The increased photosynthetic activity would, theoretically, increase CH_2O reserves in grasses. But excess of N would also stimulate the formation of amino acids and proteins to the detriment of CH_2O reserves.

Dilz (1966) working with perennial ryegrass found 28.7, 20.1, 19.0 and 16.8% of CH_2O when none, 200, 400 and 600 kg of N/ha were applied, respectively. However, no effect due to N applications was found by Ford and Williams (1973) when 280, 476 and 673 kg of N/ha were applied to 'Pangola' digitgrass and Setaria anceps cv. 'Nandi'. N levels induced 11.25, 10.77 and 10.61% of CH_2O in 'Pangola', and 9.32, 10.77 and 8.88% of CH_2O in 'Nandi', respectively.

The regrowth of 'Coastal' bermudagrass evaluated by Adegbola and McKell (1966) was closely related (r=0.72) to

the content of CH_2O reserves in the stubble and rhizomes. Nitrogen fertilization at low and moderate levels (50 and 100 kg of N/ha) stimulated leaf area expansion and chlorophyll synthesis, thus enhancing photosynthetic capacity and increasing the amount of CH_2O produced (25.3 and 25.8%), as compared to 20.4, 20.4 and 21.5% of CH_2O, as a consequence of applications of 150, 200 and 250 kg of N/ha, which stimulated protein synthesis to the detriment of CH_2O reserves.

Effect on Regrowth After Clipping

Carbohydrate accumulation in plant tissues involves a dynamic system of energy balance. There is (1) a net energy loss when CH_2O demands for growth exceeds photosynthesis; (2) CH_2O accumulates in tissues when growth demands are low, relative to fixation by photosynthesis (Blaser et al., 1966). Therefore, under environments favorable for growth, the physiological role of CH_2O in regrowth of defoliated forages may depend on the degree of defoliation and energy demand by plants.

Davidson and Milthorpe (1965) reported that current photosynthesis of Dactylis glomerata was unable to meet the demand for current growth and respiration during the first four days after defoliation. During the first two days, there must have been contributions to growth and respiration from roots, and from labile fractions in the plants.

The authors found that the rate of regrowth immediately following defoliation was related to the concentration of CH_2O present at defoliation time. However, the root extension almost ceased after severe defoliation, and was appreciably curtailed even when a high concentration of CH_2O reserve was present. Root extension and mineral uptake did not again begin until the leaves had expanded to an area which was sufficient to supply photosynthates adequate to meet all current needs. It was assumed that the reserve CH_2O forms part of a labile pool, and is used for the synthesis of new compounds and for respiration when synthesis is restricted. This labile pool contributes significantly to new growth only during the first few days following defoliation. The extent of this contribution depends on the severity of defoliation, and on the level of the environmental factors influencing growth and those influencing photosynthesis.

Bommer (1966) also verified that the relationship of CH_2O levels to regrowth after defoliation may be influenced by the stimulation of root growth after defoliation. Since root extension is otherwise closely related to uptake of mineral nutrients, N and other elements applied to the plants seem to be able to compensate for the effect of frequent defoliation in several ways, which may be only partially correlated to an increase in CH_2O reserves.

Marshall and Sagar (1965) expressed the belief that newly formed tillers of Lolium multiflorum Lam. might be dependent on mature leaves of other tillers for CH_2O supplies, and on the root system of other tillers for water and minerals. However, as soon as the new tiller produces adventitious roots and sufficient leaf area, it becomes potentially independent, even though it remains physically attached to its parent. When one undefoliated tiller remains on a plant that has been defoliated, the initial reaction to the loss of leaves is the complete breakdown of the photosynthetic independence of tillers. Intact tillers might have supported the damaged ones, by supplying both, roots and shoots with currently fixed assimilates. In spite of the apparent individuality of tillers, the reaction to defoliation indicated that they had the potential to reintegrate with all the other tillers on the plant under condition of stress.

It is suggested that following a severe defoliation, regrowth during the first week is limited by soluble CH_2O content in the bases of expanding leaves, then by the rate of photosynthesis, and further by the rate of water and nutrient uptake sustained by the root system (Davidson and Milthorpe, 1966).

A marked quadratic response of TNC reserves to grazing was reported by Adjei (1978) working with Cynodon aethiopicus Clyton & Harlan, Cynodon nlemfuensis Vanderyst. and Cynodon

aethiopicus cv. 'McCaleb' Digitaria decumbens cv. 'Pangola' and Paspalum notatum Flugge cv. 'Pensacola' in Central Florida. A regrowth period of 28 days was sufficient to recover fully the depleted TNC on all treatments. In the stargrasses, the concentration of TNC in the roots was higher than that in the stubble; however, it was greater in the stubble than in the roots of 'Pangola' digitgrass, and higher in the rhizomes than roots of 'Pensacola' bahiagrass.

It seems logical that regrowth following defoliation is a function of CH_2O reserves and photosynthetizing tissues remaining after defoliation; it is also a function of light and temperature, soil moisture, soil nutrients and season, and those factors interacting differently with each grass species and even among cultivars.

Digestibility of Forage Species

In general, the digestibility of forage plants declines with advanced maturity (Moore and Mott, 1973; Van Soest, 1973). The digestibility of temperate species declines about 0.5 percentage units per day (Reid et al., 1959), while a decrease of 0.1 to 0.2 percentage units per day occurring in tropical species was reported by Minson (1971). The higher rate of decrease in digestibility units for temperate species towards their maturity might be a real one, since tropical species start off at lower digestibility than temperate ones. However, it could also be caused by the

very much longer period over which the tropical pasture plants were studied, the nature of decline being sigmoidal rather than linear (Moore and Mott, 1973).

Correlations between in vitro digestibility of cellulose or dry matter, and in vivo digestibility of dry matter or digestible energy may be expected to be 0.90 or higher, therefore permitting a good estimate of forage digestibility (Church, 1975). As a rule, the two-stage in vitro procedure developed by Tilley and Terry (1963), modified by Moore and Mott (1974), gives a better prediction of in vivo digestibility than chemical procedures (Deinum and Van Soest, 1969; Golding et al., 1976).

In vivo digestion is appropriate to describe differences in digestibility between two forages, since these differences are the result of numerous interactions with their chemical components. Therefore, chemical and in vitro procedures should be regarded as complementary. This permits a study of forage digestibility based on nonempirical concepts (Velasquez, 1974).

Arroyu-Aguilu (1975) studying pastures of Panicum maximum, Digitaria decumbens cv. 'Pangola', Brachiaria ruziziensis, Pennisetum purpureum Schumach and Cynodon nlemfuensis harvested weekly in southern Puerto Rico, found lower digestibility values at all stages of growth than in temperate species at similar ages. 'Pangolagrass', though the lowest in IVOMD percentage, declined with advancing age, but maintained better quality for a longer period.

The IVOMD of 'Pangolagrass','Transvala' and 'Coast-cross-1' (Kien et al., 1976) were 63.2, 65.1 and 60.2%, respectively, and N applications did not affect the digestibility values. Reasonably constant IVOMD values of a 'Pangola' digitgrass sward is reported by Cowlishaw and Archibald (1972) in a 180-day grazing trial in Trinidad. They varied from 52 to 56% at each cycle of 28 days.

The digestibility of four Digitaria cultivars was studied in Florida (Sleper and Mott, 1976) at 14, 28 and 42-day harvesting intervals. Simple regression values indicated that digestibility of 'Pangola' digitgrass decreased more rapidly as the season progressed than other cultivars at 14-day harvesting frequency. The slopes were -0.69, -0.71, -0.80 and -1.02 for the cultivars 'Slenderstem', 'X50-1', 'Transvala' and 'Pangola', respectively. The smallest b value would indicate that the quality of forage is better maintained over time, since digestibility would decrease less rapidly than that associated with a higher b value. They concluded that digestibility differences do exist between the different Digitaria cultivars examined. There was, however, no difference among cultivars at 28-day harvesting frequency. It was necessary to establish these differences so that current managerial practices can be implemented to give maximum animal performance.

Crude Protein in Tropical Grasses

The generally low crude protein (CP) content in tropical grasses results in part from their inherent physiological capacity to more efficiently utilize nitrogen for dry matter production (Wilson, 1975). Coupled with this, the high potential relative growth rate of tropical grasses leads to more rapid exhaustion of available N, as it is clearly evident in studies with tropical grasses, where a rapid decline of leaf organic nitrogen is almost always observed.

The CP content of Panicum maximum, Digitaria decumbens, Brachiaria ruziziensis, Pennisetum purpureum and Cynodon nlenfuensis declined from an average 18.1% when cut at 7 days to 5.6% at 63 days (Arroyo-Aguilu et al., 1975); while the CP content of 'Pangola' digitgrass, Tannergrass, Bermudagrass, and Hexapangolagrass varied from 12.0 to 7.8% when cut at 30- or 60-day intervals, respectively (Sotomayor-Rios et al., 1974).

Milford and Haydock (1965) reported a nonlinear relationship between the decline in CP content and increase in maturity. The decline proceeded rapidly for a period of 40 to 60 days, when almost constant decreases were observed afterwards.

A marked decline in intake of tropical forages occurs when the CP content falls below 7% (Milford and Minson,

1966). A lack of CP for the rumen microflora may cause a low energy intake which is responsible for the low feeding values of several mature tropical grasses. The low CP content may also exert influence on the *in vitro* digestion by depriving the rumen fluid bacteria of some of their N requirements (Cubillos et al., 1970).

CHAPTER III

MATERIAL AND METHODS

This study was conducted at the Green Acres Farm of the Agronomy Department, University of Florida, near Gainesville, Florida, from June 29 to November 2, 1977, in an established sward of Hybrid Digitgrass 'X46-2', formerly named Digitaria decumbens Stent. 'X46-2'. This hybrid digitgrass resulted from a cross accomplished in 1965, at the University of Florida, between Digitaria x umfolozi Schank & Hall = Digitaria sp. (PI # 299892) and Digitaria valida Stent. (PI # 299850). The sward was already established in a transitional area between two soil types (Carvalho, 1976)—Kendrick loamy fine sand (loamy, siliceous, hyperthermic Arenic Paleudult) and Sparr loamy fine sand (loamy, hyperthermic, Grossarenic Paleudult).

This trial was performed to determine growth responses of the digitgrass sward to different frequencies of defoliation; digestibility of the forage produced, and to relate regrowth following defoliation to carbohydrate reserves.

Field Measurements

Dry Matter Yield

Three frequencies of defoliation, 4, 6 and 8 weeks, were imposed on the sward in four replications. The plots were

mowed on June 29 to provide a uniform stubble height (8 to 10 cm), and 60 kg of N/ha as ammonium nitrate was applied to the plots. Similar amounts of fertilizer were again broadcast at 4-week intervals to all experimental units. A schedule of defoliations is shown in Fig. 1, where A1, A2, A3 and A4 represent the four regrowth cycles under 4-week defoliation treatment; B1, B2 and B3, the three regrowth cycles under 6-week defoliation treatment; C1 and C2, the two cycles of regrowth under 8-week defoliation treatment.

After each harvest, and at every subsequent week, four samples were taken from 0.25 m^2 area, clipped at ground level, and weighed after 48 to 72 hours in a forced-air oven at drying temperatures of 60 to 65°C.

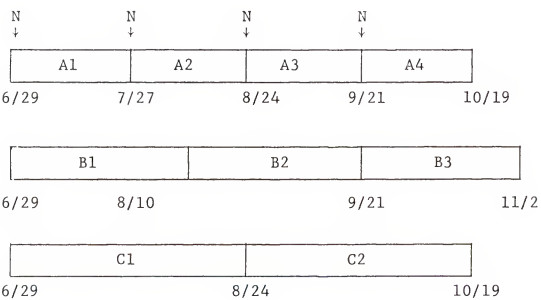

Fig. 1 Regrowth cycles under 4-week defoliation treatment (A1, A2, A3 and A4), 6-week defoliation treatment (B1, B2 and B3), and 8-week defoliation treatment (C1 and C2), and frequency of N applications.

Total Nonstructural Carbohydrates (TNC)

Samples of stem bases up to 10-cm height were collected in all regrowth cycles at the following frequencies: zero, 2, 5, 7, 14, 21 and 28 days after each harvest for treatment A; zero, 2, 5, 7, 14, 21, 28, 35 and 42 days for treatment B; and zero, 2, 5, 7, 14, 21, 28, 35, 42, 49 and 56 days for treatment C.

The number of tillers randomly collected for each sample varied from 150 to 100 according to the stage of tiller development. After cutting and removal of all leaf sheaths, the stems were kept in plastic bags, on ice, until taken to the oven for drying at 60 to 65°C.

Canopy Stratification and Leaf Area Index

Two of the four samples collected for DM yield determinations were clipped in layers of 10-cm height, and weighed after drying. From one of the four samples, subsamples were taken for leaf area determination using an Automatic Area Meter Integrator (Type AAM-5, Hayashi Denko Co.). This was done weekly for every layer, during the regrowth cycles A2, A3, A4, B2, B3 and C2 only.

Laboratory Analyses

TNC Determination

Extractions of TNC from dried and ground tissues were made according to the enzymatic procedure (Carter et al.,

1973), as modified by Adjei (1978). Briefly, 0.1 g of ground tissue was weighed into an Erlenmeyer flask and heated in boiling water bath with 5 ml of deionized water for 10 minutes to gelatinize the starch. Five milliliters of 0.2 M acetate buffer (pH 4.8) were then added to bring the volume in the flask to 10 ml of 0.1 M acetate buffer. One milliliter of the enzyme mixture was then added to digest the 0.1 g of sample in each flask. The enzyme mixture consisted of 1 ml of invertase concentrate in glycerol; 0.8 g of amyloglucosidase; 0.2 g of takadiastase; 9 ml 0.1 M of acetate buffer; 5 ml of 80% ethanol solution with a few grains of thymol dissolved; and 30 ml of deionized water. After enzyme addition, all samples were incubated at 41°C for 48 hours, and then centrifuged at 15,000 rpm for 45 minutes. The supernatant liquid containing the TNC extract was then diluted and immediately analyzed according to the Nelson-Somogyi copper reduction method (Nelson, 1944; Somogyi, 1945). Duplicate analyses were performed on each field sample.

In Vitro Organic Matter Digestion (IVOMD)

IVOMD was determined by the method of Moore and Mott (1974) based on the two-stage Tilley and Terry (1963) procedure. Organic matter rather than dry matter digestion was determined since samples in Florida are easily and almost always contaminated with sand.

Growth Analysis

The growth analysis components for this study included crop growth rate (CGR), relative growth rate (RGR), relative leaf growth rate (RLGR), and net assimilation rate (NAR) and were calculated using the formulae given by Radford (1967) as follows:

$$CGR = \frac{dW}{dT} \quad \therefore \quad \overline{CGR} = \frac{W_2 - W_1}{t_2 - t_1} \quad g/m^2/week$$

where W is the dry weight of the standing biomass, per square meter, at time t;

$$RGR = \frac{1}{W} \times \frac{dW}{dT} \quad \therefore \quad \overline{RGR} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \quad g/g/week$$

where W and t are defined as for CGR;

$$RLGR = \frac{1}{L} \times \frac{dL}{dT} \quad \therefore \quad \overline{RLGR} = \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1} \quad dm^2/dm^2/wk$$

where L is the leaf area index at the time t; and

$$NAR = \frac{1}{L} \times \frac{dW}{dT} \quad \therefore \quad \overline{NAR} = \frac{W_2 - W_1}{L_2 - L_1} \times \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1} \quad g/dm^2/wk$$

where L, W, and t are the variables already defined.

LAI was computed as follows:

$$L = \frac{A \times W \times \% \text{ leaves}}{w \times 2500},$$

where A = area of leaves, in cm^2;

W = average dry weight of four samples per plot, in grams,

w = dry weight of leaves (subsamples) from where A was obtained, in grams;

2500 = area of ground from where subsamples were obtained, in cm^2.

Besides these components of growth analysis, the effective daily temperature, or growing degrees (GD), was also calculated according to Bunting (1976) as follows:

$$GD = \frac{T_{max} - T_{min}}{2} - 10$$

where T_{max} and T_{min} are the maximum and minimum daily temperatures, respectively, observed during the experimental period, and expressed in degrees centigrade.

Statistical Analyses

Analyses of variance were computed among regrowth cycles within the same defoliation frequency using SAS ANOVA procedure (Barr et al., 1976); whereas orthogonal contrasts (Steel and Torrie, 1960) were used to compare effects due to treatments during corresponding length of

period. GLM procedures (Barr et al., 1976) were also used to develop predictive equations, and to detect associations between growth parameters. The means were always compared by Duncan's multiple range test.

CHAPTER IV

RESULTS AND DISCUSSION

Growth Analysis

Dry Matter Yield

The dry matter yield and its distribution along the successive regrowth cycles under different defoliation frequencies is shown in the Table 1, where A1, A2, A3 and A4 represent successive regrowth cycles under 4-week harvest intervals; B1, B2 and B3, the cycles under 6-week harvest frequency; C1 and C2, the regrowth cycles when the sward was harvested at 8-week intervals.

The most productive of the cycles under 4-week defoliation frequency was A2 (3,610 kg of DM/ha), followed by A1 and A3 (2,780 and 2,550 kg of DM/ha, respectively), while the cycle A4 was the least productive (1,900 kg of DM/ha). When the sward was harvested at each 6 weeks, the second regrowth cycle (B2) showed the highest production (4,800 kg of DM/ha), being different ($P<0.05$) from B1 (4,140 kg of DM/ha), which in turn were different ($P<0.05$) from cycle B3 (2,330 kg of DM/ha). On the other hand, when the sward was harvested at 8-week frequency, the first cycle C1 was more

Table 1. Dry matter yield (kg/ha), and its distribution in the successive regrowth cycles of the sward under 4-, 6- and 8-week defoliation frequencies (A, B and C, respectively).

	Regrowth cycles				
	A1	A2	A3	A4	Total
Observed†	2,780b§	3,610a	2,550b	1,900c	10,840
Produced‡	2,480a	2,620a	1,580b	970c	7,650
	B1	B2	B3		Total
Observed	4,140b	4,800a	2,330c		11,270
Produced	3,840a	3,760a	1,270b		8,870
	C1	C2			Total
Observed	5,880a	3,910b			9,790
Produced	5,580a	2,880b			8,460

†DM yield observed at the end of every regrowth cycle.

‡Observed value less the residual DM left for regrowth.

§The same means followed by the same letter in the same row did not differ by Duncan's multiple range test (P>0.05).

productive ($P<0.05$) than the following regrowth period C2, yielding 5,880 and 3,910 kg of DM/ha, respectively.

Decreased effective daily temperatures, expressed as weekly accumulated growing degrees (AcGD), and decreased accumulated rainfall (AcR) occurred during the experimental period. AcGD values (Table 2a) declined from 474 to 311°C, during regrowth cycles A1 and A4, respectively. They also declined from 714 to 448°C (Table 2b), during B1 and B3, respectively; and from 940 and 757°C (Table 2c) during the cycles C1 and C2, respectively. The amounts of rainfall available for growth were 74, 189, 140 and 21 mm (Table 2a) for cycles A1, A2, A3 and A4, respectively. Total amounts of rainfall occurred during B1, B2 and B3 were 114, 289 and 26 mm (Table 2b), respectively; whereas 263 and 161 mm of rainfall were available for cycles C1 and C2, respectively.

The weekly distribution of effective growing degrees and rainfall is shown in the Fig. 2. An almost constant decreasing rate of 0.8 units[†] per week in effective growing degrees occurred from July to October. However, beginning in October, a sharp decline of 28 units[‡] per week was observed; it increased again in the last week of the month. The rainfall distribution was quite erratic, as

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[†]GD = 120.70 -0.7981 week; r=-0.73, $S_{y.x}$=4.26, n=13

[‡]GC = 148.47 -28.2780 week; r=-0.92, $S_{y.x}$=39.49, n=4

Table 2a. Weekly accumulated growing degrees (^{o}C) and weekly accumulated rainfall (mm) during each regrowth cycle under a 4-week defoliation frequency.

	Regrowth cycles							
	A1		A2		A3		A4	
Week	AcGD	AcR	AcGD	AcR	AcGD	AcR	AcGD	AcR
	^{o}C	mm	^{o}C	mm	^{o}C	mm	^{o}C	mm
1	115	16	122	19	110	12	111	13
2	237	63	240	40	219	47	207	17
3	356	72	354	98	334	123	290	20
4	474	74	466	189	446	140	311	21

Table 2b. Weekly accumulated growing degrees (^{o}C) and weekly accumulated rainfall (mm) during each regrowth cycle under a 6-week defoliation frequency.

	Regrowth cycles					
	B1		B2		B3	
Week	AcGD	AcR	AcGD	AcR	AcGD	AcR
	^{o}C	mm	^{o}C	mm	^{o}C	mm
1	115	16	114	58	111	13
2	237	63	226	149	207	17
3	356	72	336	161	290	20
4	474	74	445	196	311	21
5	595	93	560	272	388	24
6	714	114	671	289	448	26

Table 2c. Weekly accumulated growing degrees (^{o}C) and weekly accumulated rainfall (mm) during each regrowth cycle under 8-week defoliation frequency.

	Regrowth cycles			
	C1		C2	
Week	AcGD	AcR	AcGD	AcR
	^{o}C	mm	^{o}C	mm
1	115	16	110	12
2	237	63	219	47
3	356	72	334	123
4	474	74	446	140
5	595	93	557	153
6	714	114	652	157
7	828	172	736	160
8	940	263	757	161

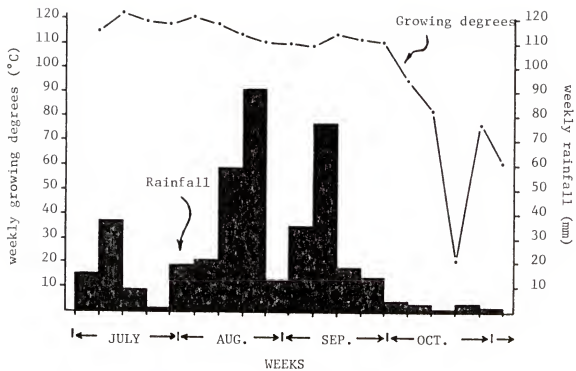

Fig. 2. Weekly distribution of growing degrees (AcGD) and rainfall (AcR) during the experimental period.

shown in Fig. 2. Amounts of rainfall during July, August and September were 83, 182 and 155 mm, respectively; while almost no rainfall (24 mm only) occurred during October. The correlation coefficient between dry matter production during all regrowth cycles and AcGD was 0.94 ($P<0.01$), whereas the correlation between AcR and yield was 0.83 ($P<0.01$). Therefore, decreased temperatures and rainfall resulted in decreased forage yields as the season progressed.

Since quality and quantity of harvestable forage are of immediate interest for animal production, another approach must be used to interpret the observed treatment effects. As stated earlier (Chapter III), the sward was harvested at about 10 cm above ground level, whereas samples to determine yield and forage quality were taken by clipping all standing biomass. Therefore, the residual dry matter left for regrowth in the cycles A2, B2 or C2, for instance, were really produced during their previous cycles A1, B1 or C1, respectively, hence, cannot be computed again as yield in the next growing period. Then, the dry matter produced in the canopy during each regrowth cycle (Table 1) was calculated by difference between observed values at the end of each cycle, and the amounts of dry matter remaining at the beginning of corresponding ones (Tables 3a, 3b and 3c).

Therefore, when the sward was harvested twice, at 8-week intervals, it produced 10.6% more dry matter than when

cut four times at 4-week intervals (8,460 and 7,650 kg of DM/ha, respectively). The amount of dry matter produced during the cycles B1, B2 and B3 until its fifth week (totaling 16 weeks) was 8,470 kg of DM/ha, being similar to the amount of forage produced during the cycles C1 + C2 (8,460 kg of DM/ha).

Orthogonal comparisons made among dry matter produced by regrowth cycles A1 + A2 vs. C1 (5,100 vs. 5,580 kg of DM/ha), A3 + A4 vs. C2 (2,550 vs. 2,880 kg of DM/ha), and A1 + A2 + A3 vs. B1 + B2 (6,680 vs. 7,600 kg of DM/ha) were all highly significant ($P<0.01$), suggesting a possible stress due to more frequent defoliation of the sward. On the other hand, 4 weeks were insufficient for the sward to achieve maximum dry matter yield under the environmental conditions, and the low level of N fertilization to which the sward was subjected. Nevertheless, the digestibility of this forage produced must also be considered, which will be discussed later.

Mean Crop Growth Rate ($\overline{CGR}$)

The yields of dry matter observed weekly in each cycle are shown in the Tables 3a, 3b and 3c. As a general trend, the values observed in cycles A2 and B2 were higher when compared to others under the same defoliation frequency Lower yields were almost always observed during the last regrowth cycle for each defoliation frequency. Except for the

Table 3a. Accumulated dry matter yield (kg/ha) from the 4-week defoliation frequency.

	Regrowth cycles			
Week	A1	A2	A3	A4
0	300b[†]	990a	970a	930a
1	800	1,310	1,140	1,195
2	1,620	1,680	1,300	1,380
3	2,690	2,730	1,970	1,690
4	2,780b	3,610a	2,550b	1,900c

[†]The means followed by the same letter in the same row did not differ by Duncan's multiple range test (P>0.05).

Table 3b. Accumulated dry matter yield (kg/ha) from the 6-week defoliation frequency.

	Regrowth cycles		
Week	B1	B2	B3
0	300b[†]	1,040a	1,060a
1	790	1,490	1,330
2	1,480	1,880	1,540
3	2,820	2,780	1,770
4	2,470	3,220	1,930
5	3,200	4,300	2,110
6	4,140b	4,800a	2,330c

[†]The means followed by the same letter in the same row did not differ by Duncan's multiple range test (P>0.05).

Table 3c. Accumulated dry matter yield (kg/ha) from the 8-week defoliation frequency.

	Regrowth cycles	
Week	C1	C2
0	300a[†]	1,030a
1	990	1,190
2	1,700	1,470
3	2,530	1,930
4	2,480	2,100
5	3,300	3,100
6	4,340	3,560
7	4,970	3,820
8	5,880a	3,910b

[†]The means followed by the same letter in the same row did not differ by Duncan's multiple range test (P>0.05).

value observed at the beginning of the experiment (weeks zero for A1, B1 and C1), dry matter residuals left for regrowth were similar ($P>0.05$) in successive cycles.

If a linear increase in dry matter yield is assumed (Table 4), the mean crop growth rate ($\overline{CGR}$) for each regrowth cycle can be calculated from prediction equations for dry matter yield, with no intercept. Thus, the rate of increase in dry matter observed during cycle A2 was 91 g/m^2/week (Fig. 3). However, the rates of increase in dry matter were lower ($P<0.05$) in the later cycles under the same defoliation frequency (66 and 55 g/m^2/week during A3 and A4, respectively). The $\overline{CGR}$ observed in B2 was twice as much as that observed in B3 (84 and 45 g/m^2/week, respectively). The rates of increase in yield during C1 and C2 were 71 and 55 g/m^2/week, respectively.

Correlation coefficients between $\overline{CGR}$ and AcGD, and between $\overline{CGR}$ and AcR were 0.73 and 0.66 ($P<0.01$), respectively, for regrowth cycles under 4-week defoliation frequency. Higher associations were observed between $\overline{CGR}$ and AcGD, and between $\overline{CGR}$ and AcR (0.82 and 0.90, respectively, at $P<0.01$) for cycles under a 6-week defoliation frequency. For cycles harvested at every 8 weeks, the correlation between $\overline{CGR}$ with both AcGD and AcR was 0.75 ($P<0.01$). These associations explain the observed decrease in $\overline{CGR}$ values with advance in the growing season, since less effective daily

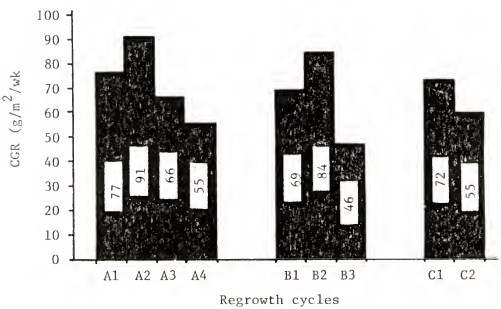

Fig. 3. Mean crop growth rate ($\overline{CGR}$), in g/m^2/week, during the growing period of each regrowth cycle.

Table 4. Prediction equations for dry matter yield (g/m^2) for each regrowth cycles.

Cycle	Prediction equations	R^2	SE	CV(%)	n
A1	DM[†] = 77.04207 week	0.97	3.38	18.78	20
A2	DM = 91.06250 week	0.94	4.98	26.40	20
A3	DM = 66.14167 week	0.91	4.76	32.87	20
A4	DM = 55.42500 week	0.86	5.18	39.96	20
B1	DM = 69.04670 week	0.97	2.49	19.15	28
B2	DM = 84.36126 week	0.97	2.79	19.09	28
B3	DM = 46.09615 week	0.88	3.32	36.79	28
C1	DM = 71.67402 week	0.99	1.54	13.47	36
C2	DM = 54.88848 week	0.96	1.80	21.12	36

[†]DM = dry matter yield (g/m^2).

temperature and less rainfall were available for growth and development of the sward canopy.

Mean Relative Growth Rate ($\overline{RGR}$)

Relative growth rate is an index of efficiency, since it is expressed as units of DM produced per unit of DM already present at any instant. As stated by Coombe (1960), and by Booysen and Nelson (1975), $\overline{RGR}$ reflects the inherent efficiency of growth processes, irrespective of plant size, providing a good basis for comparing treatment effects. In this experiment, where lengths of growing period were different, comparisons among regrowth cycles within the same defoliation frequency, instead of among treatments, were made and shown in the Fig. 4.

The efficiency of regrowth in the four cycles under 4-week defoliation frequency declined ($P<0.05$) from 0.56 (A1) to 0.18 g/g/week (A4). It varied from 0.44 to 0.13 g/g/week when the sward was harvested at 6-week intervals, whereas 0.37 and 0.17 g/g/week were observed during the regrowth cycles C1 and C2, respectively. The decreased efficiency in the rate of dry matter production in successive regrowth cycles was correlated with the effective growing degrees, $r=0.76$, $r=0.86$ and $r=0.86$ ($P<0.01$) for the cycles under 4-, 6- and 8-week defoliation frequencies, respectively.

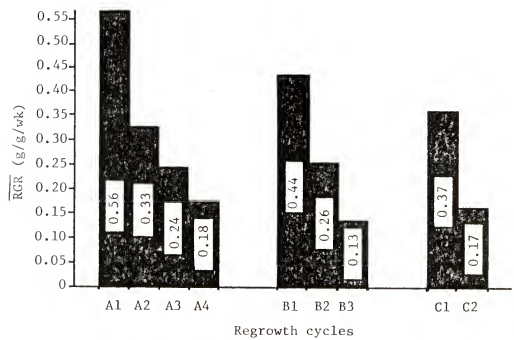

Fig. 4. Mean relative growth rate ($\overline{RGR}$), in g/g/week, during the growing period of each regrowth cycle.

The weekly variations in RGR did not follow a regular pattern. However, the lowest values (Table 5), or lower efficiency of DM production, were always observed in the last weeks of the latest regrowth cycles A4, B3 and C2.

The interpretation of experiments involving comparisons of plant performance under different conditions is made easier and more revealing when the ratio of RGR and RLGR (relative leaf growth rate) is used, instead of these parameters separately, since they can only indicate a change of one of the important processes resulting in ultimate plant form (Whitehead and Meyerscough, 1962). The smaller the ratio between RGR and RLGR (R/RL), the larger is the relative rate of leaf area increase as compared to the rate of increase in dry matter; hence, more stored assimilates were used for leaf area expansion. Conversely, the larger the ratio R/RL, the smaller was the rate of leaf area increase, thus, the greater the contribution of leaf area to the rate of dry weight increase.

The highest RLGR values were observed during the first 2 weeks of regrowth (Table 5) in all cycles as a consequence of greater light penetration downward into the canopy, which may have stimulated tillering from basal and axillary buds. The R/RL ratio was almost always the lowest in these 2 weeks rather than in the subsequent ones, when values close to or greater than unity were observed. When the ratio R/RL was

Table 5. Relative growth rate (RGR, g/g/week), relative leaf growth rate (RLGR, dm^2/dm^2/week), and the ratio RGR/RLGR (R/RL) for every week in the regrowth cycles A2, A3, A4, B2, B3 and C2.

	Regrowth cycles								
	A2			A3			A4		
Week	RGR	RLGR	R/RL	RGR	RLGR	R/RL	RGR	RLGR	R/RL
1	0.28	1.11	0.25	0.17	0.89	0.19	0.25	1.63	0.15
2	0.25	0.53	0.47	0.13	1.03	0.13	0.15	0.31	0.48
3	0.40	0.31	1.30	0.42	0.64	0.66	0.20	0.45	0.44
4	0.36	0.43	0.84	0.26	0.22	1.15	0.12	-0.12	-1.00

	B2			B3			C2		
Week	RGR	RLGR	R/RL	RGR	RLGR	R/RL	RGR	RLGR	R/RL
1	0.36	1.57	0.23	0.23	2.37	0.10	0.14	0.97	0.15
2	0.23	0.93	0.25	0.15	0.96	0.16	0.21	1.30	0.16
3	0.40	0.23	1.74	0.14	0.23	0.59	0.27	0.52	0.53
4	0.14	0.20	0.71	0.09	-0.18	-0.50	0.08	0.07	1.14
5	0.29	-0.19	-1.52	0.09	0.33	0.27	0.39	0.65	0.60
6	0.11	0.18	0.61	0.10	0.06	1.67	0.08	-0.29	-0.28
7	x	x	x	x	x	x	0.13	0.08	1.62
8	x	x	x	x	x	x	0.02	-0.19	-0.11

x = Nonexistent.

greater than unity, it meant that the plant community increased its dry weight to a greater extent than it did in the rate of leaf area expansion. However, when the ratio R/RL was close to unity, an increase in dry weight occurred, but not at the same rate as did leaf area expansion. Furthermore, when negative values were observed, the plant community lost leaf area and the rate of dry weight increase was low, or almost none, as observed later in regrowth cycles B3 and C2.

Leaf Area Index (LAI)

LAI increased linearly during the regrowth cycles A2 and A3 (Fig. 5); however, a quadratic function explained better the weekly variations in LAI during the regrowth cycles A4, B2, B3 and C2 (Table 6).

The canopy stratification, and the respective LAI value in each 10-cm layer, determined weekly, is given in the Tables 7a, 7b and 7c. A general increase in LAI, in the same layer, during successive weeks of regrowth in cycles A2, A3 and A4 was observed, although few exceptions occurred. For instance, during cycle A2, in layer 0 to 10 cm, a decrease in LAI from 0.95 to 0.74 was detected from the second to the third week. The falling of senescent leaves produced in the previous regrowth cycle A1 might explain this eventuality. A slight decrease in LAI also occurred during the third week in the 10 to 20 cm layer. Since the increase in

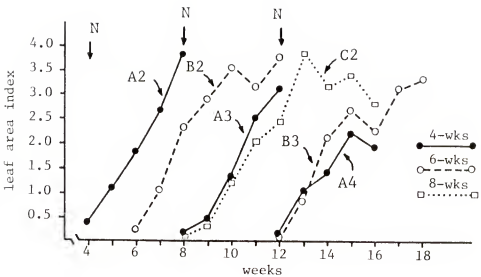

Fig. 5. Leaf area index (LAI) during the regrowth cycles A2, A3, A4, B2, B3 and C2.

Table 6. Prediction equations for LAI during the regrowth cycles A2, A3, A4, B2, B3 and C2.

Cycle	Predicted equations	R^2	CV(%)
A2	$LAI = 0.29 + 0.7987W^{\dagger}$	0.91	19.6
A3	$LAI = -0.05 + 0.7996W$	0.86	30.6
A4	$LAI = 0.18 + 0.9751W - 0.12567W^2$	0.76	30.9
B2	$LAI = 0.16 + 1.2827W - 0.11785W^2$	0.91	16.4
B3	$LAI = 0.07 + 1.0857W - 0.09383W^2$	0.84	23.9
C2	$LAI = -0.30 + 1.0466W - 0.07712W^2$	0.83	26.5

$^{\dagger}W$ = week

Table 7a. Leaf area index observed in each layer for each week in the regrowth cycles A2, A3 and A4.

Regrowth cycle A2							
	Layers (cm)						
Week	0-10	10-20	20-30	30-40	40-50	50-60	Total
0	0.36	xxxx	xxxx	xxxx	xxxx	xxxx	0.36
1	0.56	0.37	0.16	xxxx	xxxx	xxxx	1.09
2	0.95	0.59	0.30	xxxx	xxxx	xxxx	1.84
3	0.74	0.50	0.68	0.61	xxxx	xxxx	2.53
4	1.13	0.78	0.87	0.68	0.31	0.13	3.90
Regrowth cycle A3							
0	0.20	xxxx	xxxx	xxxx	xxxx	xxxx	0.20
1	0.38	0.10	xxxx	xxxx	xxxx	xxxx	0.48
2	0.97	0.37	xxxx	xxxx	xxxx	xxxx	1.34
3	1.16	0.98	0.39	xxxx	xxxx	xxxx	1.53
4	1.48	1.17	0.52	xxxx	xxxx	xxxx	3.17
Regrowth cycle A4							
0	0.20	xxxx	xxxx	xxxx	xxxx	xxxx	0.20
1	0.78	0.26	xxxx	xxxx	xxxx	xxxx	1.04
2	1.01	0.40	xxxx	xxxx	xxxx	xxxx	1.41
3	1.50	0.74	xxxx	xxxx	xxxx	xxxx	2.24
4	1.18	0.79	xxxx	xxxx	xxxx	xxxx	1.97

xxxx Nonexistent.

Table 7b. Leaf area index observed in each layer for each week in the regrowth cycles B2 and B3.

Regrowth cycle B2						
	Layers (cm)					
Week	0-10	10-20	20-30	30-40	40-50	Total
0	0.22	xxxx	xxxx	xxxx	xxxx	0.22
1	0.79	0.29	xxxx	xxxx	xxxx	1.08
2	1.37	1.04	xxxx	xxxx	xxxx	2.41
3	0.98	0.97	0.97	xxxx	xxxx	2.92
4	0.77	0.91	1.27	0.63	xxxx	3.58
5	0.44	0.57	0.80	0.99	0.43	3.23
6	0.51	0.61	0.94	1.20	0.55	3.81
Regrowth cycle B3						
0	0.08	xxxx	xxxx	xxxx	xxxx	0.08
1	0.63	0.19	xxxx	xxxx	xxxx	0.82
2	1.67	0.47	xxxx	xxxx	xxxx	2.14
3	1.90	0.81	xxxx	xxxx	xxxx	2.71
4	1.40	0.87	xxxx	xxxx	xxxx	2.27
5	2.38	0.78	xxxx	xxxx	xxxx	3.16
6	2.34	1.02	xxxx	xxxx	xxxx	3.36

xxxx Nonexistent.

Table 7c. Leaf area index observed in each layer for each week in the regrowth cycle C2.

Regrowth cycle C2					
	Layers (cm)				
Week	0-10	10-20	20-30	30-40	Total
0	0.13	xxxx	xxxx	xxxx	0.13
1	0.27	0.06	xxxx	xxxx	0.33
2	0.86	0.37	xxxx	xxxx	1.23
3	1.04	0.80	0.22	xxxx	2.06
4	1.19	1.00	0.29	xxxx	2.48
5	1.90	1.23	0.76	xxxx	3.89
6	0.74	1.16	0.86	0.41	3.17
7	0.83	1.09	0.80	0.70	3.42
8	0.72	0.77	0.87	0.48	2.84

xxxx Nonexistent.

LAI observed during this week in the 20 to 30 cm layer was twice as much as occurred in the same layer during the previous week, stem elongation might have added leaves to the upper layer, besides the appearance of new and enlargement of existent photosynthetizing tissues.

During regrowth cycle A3, LAI increased in all layers every week. This also occurred during cycle A4, except during the last week, when the canopy lost leaves in its lower layer. The LAI values obtained at the end of these cycles (Table 7a) were 3.90 (A2), 3.17 (A3) and 1.97 (A4). Significant ($P<0.01$) associations between LAI and dry matter yield, AcDG or AcR, were found ($r=0.85$, $r=0.76$ and $r=0.79$, respectively) during these regrowth cycles.

During regrowth period B2, N was applied at the beginning of the second week of growth; in fact, a sharp increase in LAI from 1.08 (week 1) to 2.41 (week 2) was observed (Table 7b), as a consequence of N fertilization. After this period a decrease in LAI occurred in 0 to 10 and 10 to 20 cm layers, until the fifth week, when the decline was most evident even in the 20 to 30 cm layer. At this time, the entire canopy had a lower LAI (3.23) than in the previous week (3.58). However, during the sixth week, LAI increased again to 3.81.

During cycle B3, a decline in LAI was recorded in the fourth week, followed by an accentuated increase. At that

particular period, the temperature declined sharply (Fig. 2), and a light frost occurred in the experimental plots, which impaired the sward canopy. Afterward, temperature rose again, which favored tillering and leaf elongation, thus, increasing LAI. The cycle started with LAI 0.08. At this time, N was applied, and LAI increased to 0.82 in one week, and to 2.14 in the next one. Probably, the greater quantity of light penetrating the sward after defoliation favored tillering from basal buds, while N enhanced stem elongation and leaf enlargement.

The regrowth cycle C2, which started after defoliation and N fertilization, showed a ninefold increase in LAI (0.13 to 1.23) from week zero until week 2 (Table 7c). Nitrogen was again applied to the sward after its fourth week of regrowth, and LAI increased from 2.48 (week 4) to 3.89 (week 5). Nonetheless, LAI values tended to decline after week 5 in this cycle, probably as a consequence of self-shading and falling of senescent leaves.

Mean Net Assimilation Rate ($\overline{NAR}$)

Net assimilation rate depends almost entirely on leaf activity. It is highly dependent on environmental factors, and less dependent on internal factors (Coombe, 1960; Ludlow and Wilson, 1970). Since NAR is equal to $1/L \times dW/dt$, leaf area should be measured as accurately as possible. However, measuring leaf area of grasses is not only a difficult task, but also a very time consuming operation subjected to many

errors. In this experiment, where only four measurements were made in each layer of the grass canopy, per week, in each regrowth cycle, these results must be viewed with caution.

Values for NAR are presented in Table 8, which show similar weekly oscillations during the cycles A2 and A3, but lower values during A4. The mean NAR values calculated during A2, A3 and A4 were 0.46, 0.36 and 0.33 g/dm^2/week, respectively, showing clearly a decline in the leaf efficiency as the season progressed.

The weekly variation in NAR values during B2 was quite erratic, whereas lower and more constant values were observed during cycle B3. Similarly, this occurred in cycle C2 after its third week, except in the fifth week, when 0.32 g/dm^2/week was observed, probably due to N applied to the sward during the previous week.

The highest NAR values always occurred during the first week of all regrowth cycles, when LAI values of 0.36, 0.20, 0.20, 0.22, 0.08 and 0.13 (Tables 7a, 7b and 7c) were observed in cycles A2, A3, A4, B2, B3 and C2, respectively. At low LAI values, almost all existent leaf area was intercepting the incoming radiation, hence, the greater leaf efficiency. Conversely, the lower NAR values observed at the end of most cycles might be the result of leaf senescence, self-shading, and leaf respiration, which were not measured in this experiment.

Table 8. Net assimilation rates (NAR), in $g/dm^2/week$, observed weekly in the regrowth cycles A2, A3, A4, B2, B3 and C2.

	Regrowth cycles					
Week	A2	A3	A4	B2	B3	C2
	$g/dm^2/week$					
1	0.48	0.55	0.31	0.82	0.36	0.75
2	0.26	0.19	0.16	0.24	0.16	0.40
3	0.48	0.36	0.17	0.35	0.10	0.29
4	0.28	0.20	0.10	0.13	0.07	0.07
5	xxx†	xxxx	xxxx	0.32	0.07	0.32
6	xxxx	xxxx	xxxx	0.05	0.07	0.07
7	xxxx	xxxx	xxxx	xxxx	xxxx	0.14
8	xxxx	xxxx	xxxx	xxxx	xxxx	0.03
$\overline{NAR}$‡	0.46	0.36	0.33	0.51	0.31	0.43

†Nonexistent.

‡Mean NAR during the regrowth cycle.

Total Nonstructural Carbohydrates (TNC)

The variations in TNC concentrations, at stem bases of the grass, followed a similar pattern during most of the regrowth cycles (Figs. 6a, 6b and 6c).

The TNC concentration observed in the sward at the beginning of the experimental period was 13.2% (Table 9). It decreased to 11.3% after 2 days of defoliation, and increased up to 23.7% in the 28th day of regrowth.

Whenever a defoliation occurred, a sharp decline in TNC contents was evident during the 5 days following defoliation (Figs. 6a, 6b and 6c). The rate of decline observed during regrowth cycles A2, A3, A4, B2, B3 and C2 were 2.9, 1.9, 1.7, 1.9, 3.3 and 2.0% per day, respectively. Several investigations have reported analogous trends in the depletion of TNC after defoliations (Bender and Smith, 1973; Blaser et al., 1966; Brown and Blaser, 1975; Ward and Blaser, 1961; Wilson and Ford, 1973). This depletion reaches a minimum (5.5 to 9.4%) at about 1 week of regrowth, followed by an increase in TNC concentrations associated with increasing photosynthetic activity (Alberda, 1966). In fact, an increase in TNC concentrations from 9.4 to 16.0, 6.2 to 16.4 and from 7.4 to 16.0% were observed during cycles A2, A3 and A4, respectively, from the 5th until the 28th day of regrowth (Table 9), while linear increases in LAI and in dry matter yield were recorded, concurrently.

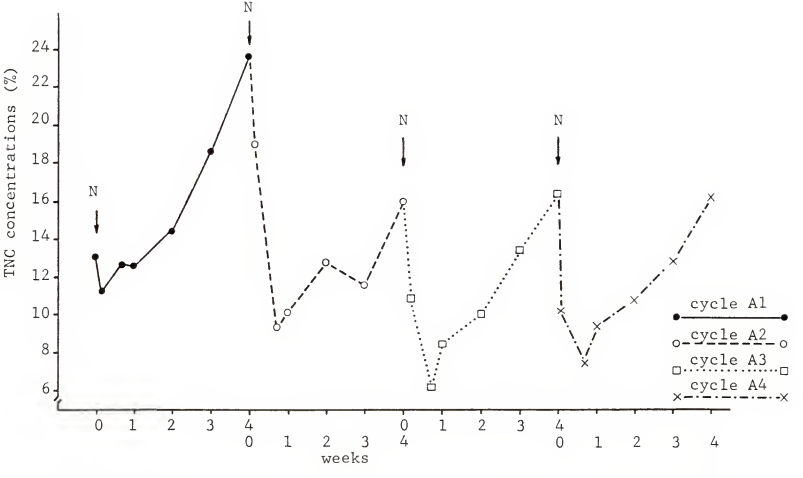

Fig. 6a. Variations in TNC concentrations (%) of herbage stem bases during regrowth cycles A1, A2, A3 and A4.

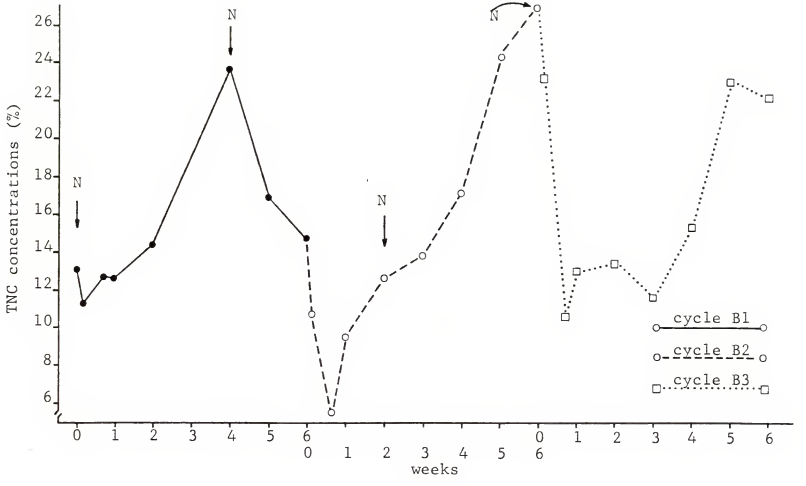

Fig. 6b. Variations in TNC concentrations (%) of herbage stem bases during regrowth cycles B1, B2 and B3.

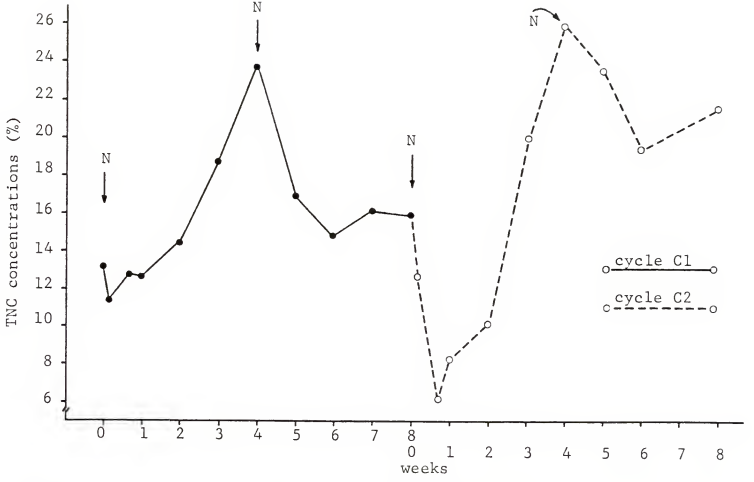

Fig. 6c. Variations in TNC concentrations (%) of herbage stem bases during regrowth cycles C1 and C2.

Table 9. Total nonstructural carbohydrate (%) at stem base during the regrowth cycles A1, A2, A3, A4, B1, B2, B3, C1 and C2.

	Regrowth cycles								
Days	A1	A2	A3	A4	B1	B2	B3	C1	C2
	%								
0	13.2	23.7	16.0	16.4	13.2	14.8	26.9	13.2	15.8
2	11.3	19.5	10.9	10.3	11.3	10.8	23.2	11.3	12.6
5	12.7	9.4	6.2	7.4	12.7	5.5	10.7	12.7	6.1
7	12.7	10.1	8.5	9.3	12.7	9.5	13.1	12.7	8.2
14	14.4	12.8	10.2	10.6	14.4	12.6	13.5	14.4	10.1
21	16.7	11.4	13.5	12.8	16.7	13.8	11.7	16.6	19.8
28	23.7	16.0	16.4	16.0	23.7	17.1	15.2	23.7	25.9
35	xxx	xxx	xxx	xxx	16.9	24.4	23.1	16.9	23.5
42	xxx	xxx	xxx	xxx	14.8	26.9	22.0	14.8	19.4
49	xxx	xxx	xxx	xxx	xxx	xxx	xxx	16.1	20.8
56	xxx	xxx	xxx	xxx	xxx	xxx	xxx	15.8	21.5

xxx Nonexistent.

During cycles B1, C1 and C2, when N was applied to the swards after their 28th day of regrowth, TNC concentrations decreased in the herbage plants. Nonetheless, similar trends were found for 'Pangola' digitgrass and Setaria anceps cv. 'Nandi' (Ford and Williams, 1973); for 'Coastal' bermudagrass (Adegbola and McKell, 1966), and for Fescue and Dallisgrass (Brown and Blaser, 1975) after N fertilizations. Curiously, an increase in TNC concentration in the herbage was observed after the application of N during cycle B2 in its second week of regrowth (Fig. 6b). During the next week, the sward increased its dry weight by 0.40 g/g (RGR), while the relative rate of leaf increase (RLGR) was 0.23 dm^2/dm^2 (Table 5, cycle B2, week 3). Therefore, the ratio R/RL, which was 1.74 at this time, supports the inference that the plant community increased its dry weight to a greater extent than leaf area expansion. Consequently, an excess of TNC could have been produced and accumulated, as it was detected at herbage stem base. TNC concentration increased from 12.6 to 13.8% (Table 9, cycle B2, days 14 and 21, respectively), instead of declining as sometimes has been reported in the literature.

Most of the time, N was applied after defoliation, thus, both N and defoliation were confounding factors inducing TNC depletion. However, as shown in Table 10, the swards during cycles A3 and C2 started their regrowth with similar

TNC concentrations (16.0 and 15.8%, respectively) in the herbage stem base. The rate of TNC depletion (1.9 and 2.0%/day) and the RGR (0.17 and 0.14 g/g) were similar during the first week of regrowth. On the other hand, the swards, during cycles A2 and B3, which started with higher TNC concentrations (23.7 and 26.9%, respectively), increased their dry weight during the first week of regrowth to a greater extent (0.28 and 0.23 g/g, respectively) than occurred during similar periods in cycles A3 and C2.

Table 10. TNC concentration in the beginning of regrowth cycle, its rate of depletion/day, and rate of dry-weight increase during the first week.

Cycle	TNC (%)	Depletion per day (%)	RGR (g/g)
A3	16.0	1.90	0.17
C2	15.8	2.00	0.14
A2	23.7	2.90	0.28
B3	26.9	3.30	0.23

During cycles B1, C1 and C2, when N was applied after 4 weeks of sward regrowth, TNC concentrations declined from 23.7 to 16.9, from 23.7 to 16.9 and from 25.9 to 23.5%, respectively, in 1 week (Table 9); while the rates of increase

in dry weight during the following week were 0.26, 0.29 and 0.40 g/g, respectively.

Therefore, when defoliation and N application occurred concomitantly, higher rates of dry weight increase resulted from swards with higher rather than lower TNC reserves. Furthermore, when N was applied far from defoliations, a transitory TNC depletion occurred, but the rates of dry weight increase during the following week were also higher.

Unfortunately, N application after 2 weeks of sward regrowth occurred only once, i.e., during cycle B2. At this time, TNC reserves increased from 12.6 to 13.8% (Table 9) in 1 week, while the rate of canopy dry weight increase was 0.40 g/g during this week.

Therefore, it would probably be better to apply N after 2 weeks of regrowth, instead of immediately after forage utilization or harvesting.

The minimum TNC required for regrowth of digitgrass 'X46-2' has never been determined under field conditions. Nevertheless, 13.2% of TNC appeared to be sufficient for regrowth of swards when harvested at 4-week intervals. A regrowth period of 28 days was sufficient to recover fully the depleted TNC concentration in stargrasses, 'Pangola' digitgrass and 'Pensacola' bahiagrass (Adjei, 1978), grazed in Central Florida at different stocking rates.

In Vitro Organic Matter Digestion (IVOMD)

Production of dry matter by any sward is only a crude expression of its potential to produce animal feed. However, its nutritive value must also be considered. Forage quality is estimated by the output per animal which is a function of voluntary intake and digestibility of nutrients when forage is fed alone, and ad libitum, to specified animals (Moore and Mott, 1973). Since IVOMD is a satisfactory predictor of forage quality, the inclusion of this parameter is of paramount importance in pasture management studies.

When the forage was harvested at 4-week intervals, its digestibility decreased from 61 to 56% (Table 11a), as observed at the end of A1 and A4, respectively. After each 6 weeks of regrowth, IVOMD values were, successively, 57, 58 and 48% (Table 11b), whereas the values observed in the herbage at the end of the regrowth cycles C1 and C2 were 51 and 50, respectively (Table 11c).

The lowest IVOMD values occurred almost always at the beginning of the regrowth cycles, coinciding with the lowest observed LAI values (Tables 7a, 7b and 7c). As LAI increased, IVOMD also increased up to the fourth week of regrowth in most of the cycles; however, decreasing LAI and IVOMD values occurred afterwards.

Table 11a. Weekly variations in herbage IVOMD (%) during the regrowth cycles A1, A2, A3 and A4.

	Regrowth cycles			
Week	A1	A2	A3	A4
		%		
0		56	44	45
1	62	56	42	52
2	67	57	52	53
3	64	63	55	53
4	61a†	61a	56a	57a

†The means followed by the same letter in the last row-week 4-did not differ by Duncan's multiple range test (P>0.05).

Table 11b. Weekly variations in the herbage IVOMD (%) during the regrowth cycles B1, B2 and B3.

	Regrowth cycles		
Week	B1	B2	B3
		%	
0		50	38
1	62	48	37
2	67	64	42
3	64	63	48
4	61	62	51
5	60	60	47
6	57a†	58a	48b

†The means followed by the same letter in the last row-week 6-did not differ by Duncan's multiple range test (P>0.05).

Table 11c. Weekly variations in the herbage IVOMD (%) during the regrowth cycles C1 and C2.

Week	Regrowth cycles	
	C1	C2
	---------- % ----------	
0		35
1	62	31
2	67	40
3	64	48
4	61	50
5	60	53
6	57	54
7	57	49
8	51a[†]	50b

[†]The means followed by different letter in the last row—week 8—were different by the F test ($P<0.05$).

During cycle A2 (Table 12a), IVOMD decreased in each layer at each subsequent week of regrowth. Higher values were always observed in the upper layers where young and tender tissues were present; whereas the lowest values occurred in the lower layers, as a consequence of lower leaf/stem ratio, and of senescent leaves. Increased digestibility values were observed in the 0 to 10 cm layer during cycles A3 and A4, since LAI also increased during the regrowth period. However, decreasing IVOMD values were observed, after the fourth week of regrowth, during cycles B2 (Table 12b) and C2 (Table 12c). This occurred mostly as an outcome of falling senescent leaves, since decreased LAI values were also observed in these layers (Tables 7b and 7c).

However, as stated earlier, both forage quality and quantity are determinants of maximum animal output per area insofar as nutrition is concerned. Therefore, during 16 weeks of regrowth, the sward produced 7,650 kg of DM/ha (Table 13) when harvested each 4 weeks; nevertheless, only 4,110 kg of total digestible organic matter (TDOM) were available to the ruminants. On the other hand, when the sward was harvested twice at 8-week intervals, during the same period, total DM produced was 8,460 kg/ha, yielding only 3,880 kg of TDOM/ha.

Table 12a. IVOMD (%) of the herbage in each layer each week in the regrowth cycles A2, A3 and A4.

Week	0-10	10-20	20-30	30-40	40-50	50-60	Standing biomass
	Regrowth cycle A2						
	Layers (cm)						
	%						
0	56	x	x	x	x	x	56
1	54	70	75	x	x	x	56
2	52	73	75	x	x	x	57
3	48	64	68	68	x	x	63
4	51	65	62	63	61	83	61
	Regrowth cycle A3						
	%						
0	44	x	x	x	x	x	44
1	41	61	x	x	x	x	42
2	50	70	x	x	x	x	52
3	57	72	68	x	x	x	55
4	49	67	70	x	x	x	56
	Regrowth cycle A4						
	%						
0	45	x	x	x	x	x	45
1	48	74	x	x	x	x	52
2	51	75	x	x	x	x	53
3	51	70	x	x	x	x	53
4	56	71	x	x	x	x	57

x Herbage nonexistent.

Table 12b. IVOMD (%) of the herbage in each layer each week in the regrowth cycles B2 and B3.

Regrowth cycle B2						
	Layers (cm)					
Week	0-10	10-20	20-30	30-40	40-50	Standing biomass
	%					
0	50	x	x	x	x	50
1	43	72	x	x	x	48
2	54	71	x	x	x	64
3	49	67	70	x	x	63
4	49	61	63	66	x	62
5	47	59	63	64	63	60
6	43	55	59	64	64	58

Regrowth cycle B3						
	%					
0	38	x	x	x	x	38
1	36	53	x	x	x	37
2	38	67	x	x	x	42
3	47	66	x	x	x	48
4	45	70	x	x	x	51
5	47	64	x	x	x	47
6	47	63	x	x	x	48

x Herbage nonexistent.

Table 12c. IVOMD (%) of the herbage in each layer each week in the regrowth cycle C2.

Week	0-10	10-20	20-30	30-40	Standing biomass
	----------	----------	% ----------	----------	
0	35	x	x	x	35
1	34	42	x	x	31
2	37	63	x	x	40
3	43	66	70	x	48
4	46	66	69	x	50
5	44	60	69	x	53
6	42	62	66	68	54
7	40	58	64	68	49
8	41	57	61	61	50

x Herbage nonexistent.

Table 13. Dry matter produced (DMP), total digestible organic matter (TDOM), and their distribution in the successive regrowth cycles (in kg/ha).

	Regrowth cycles				
	A1	A2	A3	A4	Total
DMP	2,480a	2,620a	1,580b	970c	7,650
TDOM	1,370a	1,450a	800b	490c	4,110
	B1	B2	B3		Total
DMP	3,830a	3,760a	1,270b		8,860
TDOM	1,970a	1,960a	550b		4,480
	C1	C2			Total
DMP	5,580a	2,880b			8,460
TDOM	2,580a	1,290b			3,870

† Dry matter produced (from Table 1).

†† The means followed by the same letter in the same row did not differ by Duncan's multiple range test (P>0.05).

An orthogonal comparison between TDOM produced under the 4- and 8-week harvest frequencies (4,110 vs. 3,880 kg of TDOM/ha, respectively) was different ($P<0.01$). Similarly, comparisons were made between the contrasts A1 + A2 + A3 vs. B1 + B2 (3,620 vs. 3,930 kg of TDOM/ha), and between A1 + A2 + A3 + A4 vs. B1 + B2 + B3 until its fourth week of regrowth (4,110 vs. 4,360 kg of TDOM/ha), and each was different ($P<0.01$). Nonetheless, hybrid digitgrass 'X46-2' swards under similar environmental conditions (correlation coefficients between TDOM with effective growing degrees and rainfall were 0.91 and 0.84, respectively, at $P<0.01$) and, under low levels of fertilization, would show best potential for TDOM production if utilized at every 6 weeks during the growing season.

CHAPTER V

SUMMARY AND CONCLUSIONS

Growth analysis of Hybrid Digitgrass 'X46-2' sward established in a loamy fine sand soil at Green Acres Farm, Gainesville, Florida, was performed from July to November, 1977; with the objective to determine growth reponses of the sward to different defoliation frequencies, forage quality, and to relate regrowth following defoliation to carbohydrate reserves. At the beginning of the experiment, the sward was mowed to a 10-cm stubble height. At this time, and at 4-week intervals, 60 kg of N/ha was applied. Three frequencies of defoliation were imposed on the sward in four replications, resulting in four regrowth cycles (A1, A2, A3 and A4) when the forage was harvested at 4-week intervals; in three regrowth cycles (B1, B2 and B3) when the forage was harvested at 6-week intervals; and in two regrowth cycles (C1 and C2) at 8-week defoliation frequency.

Four samples of 0.25 m^2 were clipped weekly at ground level for dry matter yield determinations. During all regrowth cycles, except A1, B1 and C1, two of these samples were cut in 10-cm layers. From one sample, subsamples were taken for leaf area measurements. These samplings generated data for growth analysis. The parameters measured were crop growth rate (CGR), relative growth rate (RGR), relative leaf growth

rate (RLGR), the ratio RGR/RLGR, leaf area index (LAI) and net assimilation rate (NAR).

Samplings to quantify total nonstructural carbohydrates (TNC) of stem bases were taken at frequencies of zero, 2, 5 and 7 days, and then, at each subsequent week until the end of each regrowth cycle.

IVOMD was determined weekly in all standing biomass, and in the forage from each layer in all regrowth cycles.

Crop growth rate (CGR) of the sward decreased as the season progressed as a consequence of decreased effective growing degrees and rainfall during the experimental period.

The efficiency of regrowth (RGR) decreased drastically from 0.56 to 0.13 g/g/week towards the end of the growing season. Weekly variations were quite erratic, although low and almost constant values (0.09 g/g/week) were observed late in the growing season.

LAI increased linearly until the fourth week of regrowth in all cycles, when decreasing LAI was observed. At the end of cycle B3, an increase in effective growing degrees resulted in increased LAI.

NAR values also decreased during the experimental period. Highest values were always observed during the first week of regrowth when, at low LAI values, almost the entire leaf was intercepting light energy. The lowest NAR values occurred at the end of most cycles, where leaf senescence, self-shading and leaf respiration were reducing leaf efficiency.

TNC concentrations at stem bases decreased sharply during the first 5 days of regrowth in each cycle as a consequence of defoliation. After 5 days, a rapid accumulation of TNC occurred. Nitrogen clearly decreased TNC concentration in stem bases of the herbage when applied on the sward after 4 weeks of regrowth during B1, C1 and C2, although no effect was apparent when it was applied after 2 weeks of herbage growth during cycle B2. These findings suggested that it would probably be better to apply N after 2 weeks of regrowth, instead of immediately after forage utilization or harvesting.

Herbage IVOMD varied from 61 to 48% at the end of regrowth cycles. Higher values occurred in the herbage harvested at 4-week intervals, whereas lower digestibilities were observed at longer growing periods, or late in the season. The lowest IVOMD values were always observed in the 0 to 10 cm layer, where low LAI values were also occurring. IVOMD values greater than 70% were recorded in upper layers during some regrowth cycles.

APPENDIX

Table 14. Analysis of variance for dry matter yield observed at the end of regrowth cycles under 4-week harvest intervals.

Source of variation	DF	Mean squares	Std. Dev.	CV(%)
Cycles (A1,A2,A3,A4)	3	5,012.55**	12.51	18.47
Replications	3	151.21		
Cycle x Replication	9	202.36		
Error	48	151.92		

**Significant at P<0.01

Table 15. Analysis of variance for dry matter yield observed at the end of regrowth cycles under 6-week harvest intervals.

Source of variation	DF	Mean squares	Std. Dev.	CV(%)
Cycles (B1, B2, B3)	2	16,419.67**	13.86	14.77
Replications	3	101.91		
Cycle x Replication	6	89.01		
Error	36	188.23		

**Significant at P<0.01

Table 16. Analysis of variance for dry matter yield observed at the end of regrowth cycles under 8-week harvest intervals.

Source of variation	DF	Mean squares	Std. Dev.	CV(%)
Cycles (C1, C2)	1	19,478.45**	19.94	16.29
Replications	3	199.78		
Cycle x Replication	3	336.59		
Error	24	410.19		

**Significant at P<0.01

Table 17. Analysis of variance for dry matter yield observed at the end of all regrowth cycles.

Source of variation	DF	Mean squares	Std. Dev.	CV(%)
Regrowth cycles	8	66,498.07**	26.90	7.59
Replications	3	511.30		
Error	24	723.38		

**Significant at P<0.01

Table 18. Analysis of variance for dry matter produced (observed less residuals) during regrowth cycles under 4-week harvest intervals.

Source of variation	DF	Mean squares	Std. Dev.	CV(%)
Cycles (A1,A2,A3,A4)	3	2,346,140.29**	271.51	14.19
Replications	3	125,322.92		
Error	9	73,717.36		

**Significant at P<0.01

Table 19. Analysis of variance for dry matter produced (observed less residuals) during regrowth cycles under 6-week harvest intervals.

Source of variation	DF	Mean squares	Std. Dev.	CV(%)
Cycles (B1, B2, B3)	2	8,549,598.00**	173.96	5.89
Replications	3	507,036.11		
Error	6	30,263.19		

**Significant at P<0.01.

Table 20. Analysis of variance for dry matter produced (observed less residuals) during regrowth cycles under 8-week harvest intervals.

Source of variation	DF	Mean squares	Std. Dev.	CV(%)
Cycles (C1, C2)	1	14,624,746.28**	351.97	8.32
Replications	3	83,433.33		
Error	3	123,883.33		

**Significant at P<0.01

Table 21. Analysis of variance for dry matter produced (observed less residuals) during all regrowth cycles.

Source of variation	DF	Mean squares	Std. Dev.	CV(%)
Regrowth cycles	8	8,529,214.33**	262.75	9.46
Replications	3	112,712.96		
Error	24	69,038.48		

**Significant at P<0.01

Table 22. Analysis of variance for crop growth rate (CGR) during regrowth cycles under 4-, 6- and 8-week harvest intervals.

Source of variation	DF	Mean squares	Std.Dev.	CV(%)
Cycles (A1,A2,A3,A4)	3	974.57**	6.10	8.39
Replications	3	77.19		
Error	9	37.20		
Cycles (B1, B2, B3)	2	1,482.19**	3.82	5.74
Replications	3	17.21		
Error	6	14.56		
Cycles (C1, C2)	1	324.61**	5.46	8.36
Replications	3	53.04		
Error	3	29.79		

**Significant at P<0.01

Table 23. Analysis of variance for relative growth rate (RGR) during regrowth cycles under 4-, 6- and 8-week harvest intervals.

Source of variance	DF	Mean Squares	Std.Dev.	CV(%)
Cycles (A1,A2,A3,A4)	3	0.0435**	0.04	13.73
Replications	3	0.0016		
Error	9	0.0016		
Cycles (B1, B2, B3)	2	0.0458**	0.05	20.69
Replications	3	0.0028		
Error	6	0.0025		
Cycles (C1, C2)	1	0.0166**	0.02	11.68
Replications	3	0.0012		
Error	3	0.0006		

**Significant at P<0.01

Table 24. Analysis of variance for dry matter residuals left for regrowth for all regrowth cycles.

Source of variation	DF	Mean squares	Std.Dev.	CV(%)
Cycles (A1,A2,A3,A4)	3	441,188.97**	66.86	8.63
Replications	3	22,629.17		
Error	9	4,741.67		
Cycles (B1, B2, B3)	2	747,384.50**	83.91	10.49
Replications	3	3,507.64		
Error	6	7,040.97		
Cycles (C1, C2)	1	1,066,939.10**	88.01	13.23
Replications	3	7,761.46		
Error	3	7,761.46		

**Significant at P<0.01

Table 25. Analysis of variance for IVOMD for all standing biomass at the end of each cycle under 4-, 6- and 8-week harvest intervals.

Source of variation	DF	Mean Squares	Std. Dev.	CV(%)
Cycles (A1,A2,A3,A4)	3	32.41	4.85	8.23
Replications	3	8.74		
Error	9	23.48		
Cycles (B1, B2, B3)	2	105.28*	3.78	6.96
Replications	3	0.54		
Error	6	14.32		
Cycles (C1, C2)	1	4.67	2.19	4.31
Replications	3	36.70		
Error	3	4.79		

*Significant at $P<0.05$

Table 26. Correlation coefficients between dry matter yield and accumulated growing degrees, and between dry matter yield and accumulated rainfall.

	AcGD	ACR	N
DM (A1,A2,A3,A4)	0.92**	0.84**	16
DM (B1, B2, B3)	0.92**	0.82**	18
DM (C1, C2)	0.97**	0.86**	16
DM (all cycles)	0.91**	0.83**	36

**Significant at $P<0.01$

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Agronomy

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